

the selected clone. On the other hand, certain genotypical properties could be an invincible barrier for the establishment and regeneration potential of some trees.

Another regeneration principle like somatic embryogenesis would lead to the same problem as organogenesis. According to our experiences the genotype, in addition to the age of the explants, is the decisive criterion which determines whether explants (in our case zygotic embryos) are suitable for induction of embryogenetic cultures and for differentiation for somatic embryos or not.

Among other things the genotype may affect endogenous hormone activity (THORPE, 1978). Therefore, it can be assumed that the clone B-8, which responds very fast in the presence of IAA, contains or metabolizes more auxins like IAA or its derivatives than B-9. All of the conditions tested to improve the response of B-9 (for example to get a more efficient multiplication of the buds) failed. A higher multiplication rate and/or induction of callus could not be achieved. This means that the effect on the endogenous level of hormones could not be the only influence of the genotype which determines propagation and regeneration potential.

The extensive research on phenotypical properties (morphology, isoenzyme pattern and so on) would allow an early selection of suitable genotypes for tissue culture but would not allow to overcome the inaccessibility of some genotypes for *in vitro* cultivation.

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## Gains in Fusiform Rust Resistance and Height Growth in a Second Generation Slash Pine Seedling Orchard

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#### Summary

In 1979, seedlings obtained from wind-pollinated slash pines in a first-generation clonal seed orchard, from a second-generation seedling seed orchard established with polymix progenies from the clonal orchard, and from an unimproved check lot were planted in a progeny test. The study was installed on one site on the Upper Coastal Plain (UCP) and one site in the Flatwoods of Georgia. The UCP test site showed more differences among seedlings lots than did the other site, especially for fusiform rust. The clonal orchard produced seedlings more susceptible to rust than the check seedlings. Seedlings from the seedling seed orchard, however, were considerably more resistant to rust than were the check or the clonal orchard lots. Gains in height growth were obtained at all stages of selection for the first- and second-generation seed orchards. Gains

in rust resistance were obtained where progeny testing for the trait was included in the selection process.

*Key words:* *Pinus elliottii* var. *elliottii*, *Cronartium quercum* f. *sp. fusiforme*, selection, breeding.

#### Introduction

When major tree improvement programs for the southern pines were begun in the 1950's, tree size and form were considered to be the most important traits that could readily be evaluated on candidate and comparison trees in natural or planted stands. Even those who were concerned about resistance to southern fusiform rust (caused by *Cronartium quercuum* (BERK.) MIYABE ex SHIRAI f. *sp. fusiforme*) had no practical way to evaluate resistance. Candidate trees with rust infections were avoided, but past

exposure to the fungus generally could not be determined. Since then, research has shown that a candidate tree's resistance to fusiform rust has not been adequately challenged unless it has grown where the hazard of infection is high (GODDARD et al., 1975).

With the dramatic increase in pine plantation acreage in the South has come an equally dramatic increase in fusiform rust incidence. The disease is the most serious problem in plantations of loblolly (*Pinus taeda* L.) and slash (*P. elliottii* ENGELM. var. *elliottii*) pines in much of the South (ANDERSON et al., 1986; CZABATOR, 1971; POWERS et al., 1975). Slash pines suffer especially high mortality rates if their stems are infected during the first few years after planting (SLUDER, 1977).

Genetics research, however, shows that some slash pines possess genetically controlled resistance to fusiform rust. The potential appears to be high for gains in resistance

through selection and breeding (BARBER, 1961; DORMAN, 1976; GRIGGS and WALKINSHAW, 1982; HODGE et al., 1989; KRAUS, 1973; SLUDER, 1975a and b, 1986, 1989; WEBB and BARBER, 1966).

In commercial tree improvement programs, 2 types of seed orchards are used to produce seeds from selected trees, orchards of clonal or seedling origin. Clonal orchards produce seeds sooner after establishment, but seedling orchards may have greater genetic improvement because selection is used in the thinning stage. This study compares the performance of progenies from both seed orchard types established in Georgia from first-generation selections of slash pine.

#### Material and Methods

In the 1950's the Georgia Forestry Commission established 2 clonal seed orchards from 149 selected slash pines.

Table 1. — Description of seed lots in the study.

Seed lot	Description
3439	60 <sup>1</sup> x wind (5-ramet mix), first-generation clone
3440	(60 x polymix) x wind (15-tree mix), second-gen. bulk
3441	(60 x polymix) x wind, second-gen. tree
3442	(60 x polymix) x wind, second-gen. tree
3443	(60 x polymix) x wind, second-gen. tree
3444	(60 x polymix) x wind, second-gen. tree
3445	119 x wind (5-ramet mix), first-gen. clone
3446	(119 x polymix) x wind (5-tree mix), second-gen. bulk
3447	(119 x polymix) x wind, second-gen. tree
3448	(119 x polymix) x wind, second-gen. tree
3449	(119 x polymix) x wind, second-gen. tree
3450	94 x wind (2-ramet mix), first-gen. clone
3451	(94 x polymix) x wind (6-tree mix), second-gen. bulk
3452	(94 x polymix) x wind, second-gen. tree
3453	(94 x polymix) x wind, second-gen. tree
3454	(94 x polymix) x wind, second-gen. tree
3455	50 x wind (4-ramet mix), first-gen. clone
3456	(50 x polymix) x wind (6-tree mix), second-gen. bulk
3457	(50 x polymix) x wind, second-gen. tree
3458	(50 x polymix) x wind, second-gen. tree
3459	(50 x polymix) x wind, second-gen. tree
3460	20 x wind (5-ramet mix), first-gen. clone
3461	(20 x polymix) x wind (3-tree mix), second-gen. bulk
3462	(20 x polymix) x wind, second-gen. tree
3463	(20 x polymix) x wind, second-gen. tree
3464	71 x wind (3-ramet mix), first-gen. clone
3465	(71 x polymix) x wind (3-tree mix), second-gen. bulk
3466	(71 x polymix) x wind, second-gen. tree
3467	6 x wind (5-ramet mix), first-gen. clone
3468	(6 x polymix) x wind (4-tree mix), second-gen. bulk
3469	76 x wind (4-ramet mix), first-gen. clone
3470	(76 x polymix) x wind (4-tree mix), second-gen. bulk
3471	Seedling seed orchard bulk, 1975
3472	Seedling seed orchard bulk, 1976
2561	Commercial seed collection (GCIA)
2562	Clonal orchard collection (GCIA)

<sup>1</sup>) GFC serial numbers of clones in the orchard.

Table 2. — Overall analyses of variance of tenth-year data, showing mean squares and significance tests, for the 2 plantings analyzed separately and combined.

Source of variation	Degrees of freedom <sup>1</sup>	Trait			
		Survival	Rust-free	Height	D.b.h.
<u>Upper Coastal Plain</u>					
Block	4	73.73	261.91*	2.21**	3.94**
Seed lot	34	316.37 **	837.08**	0.83**	1.49**
Error	133	105.07	86.34	0.19	0.58
<u>Flatwoods</u>					
Block	4	2,295.58**	63.07	10.08**	6.26**
Seed lot	35	253.82*	292.85	1.04*	2.00**
Error	135	156.60 <sup>2</sup>	215.44	0.59	1.25
<u>Two sites combined</u>					
Site	1	14,915.70**	157,918.55**	406.32**	772.84**
Block (site)	8	1,119.61	161.61	5.70**	4.65**
Seed lot	34	367.71	813.74**	1.19	1.94
Site x lot	34	206.34*	314.42**	0.71*	1.62**
Pooled error	264	132.58 <sup>3</sup>	147.82	0.39	0.90

\*) Significant at the 0.05 level.

\*\*\*) Significant at the 0.01 level.

<sup>1</sup>) Error degrees of freedom reflect a few missing plots.

<sup>2</sup>) Error degrees of freedom for survival is 138.

<sup>3</sup>) Error degrees of freedom for survival is 267.

The Commission, in cooperation with the USFS's South-eastern Forest Experiment Station, control-pollinated the clones for progeny testing. The first progeny tests, planted in 1961, included a plantation designed for conversion to a seedling-origin seed orchard.

The progenies in the second-generation seedling seed orchard were from controlled pollinations on 17 of the clones in the first-generation clonal orchard. A pollen mix from 30 other clones in the orchard was used on these 17. The 17 polymix progenies or families produced were planted in a replicated design at Georgia Forestry Commission's Arrowhead Seed Orchard in Pulaski County. At age 5 years, overall survival was 51%, and 45% of the survivors had at least one fusiform rust infection. Roguing during 1967 to 1974 reduced the number of trees from the 1,346 surviving to 141, or 10.5% of the survivors. Trees were rouged on the basis of disease, growth, form, spacing, and flower production. One family was eliminated in 1974, leaving 16.

When roguing was completed, a study was designed to quantify gains made in this second-generation seedling seed orchard. Included in the study were orchard bulk, family bulk, and individual-tree seed lots from the seedling seed orchard; and orchard bulk and individual-clone lots from the clonal orchard. All lots were wind-pollinated seeds, collected by individual tree or clone.

There were 2 seedling seed orchard bulk lots, 1 from 1975 and 1 from 1976 seed. The 1976 seed crop was more than 4 times as large as the 1975 crop. From the 1976 collection, 8 family bulk lots were formed by mixing seeds from several trees in each family. Sixteen individual-tree lots (1976 seed) from these eight families also were used, for a total of 26 seed lots from the seedling seed orchard.

For the clonal orchard lots, seeds were collected from the parent clones of the eight seedling seed orchard families mentioned above. By the time these seeds were

collected, the clonal orchard had been rouged of clones proven inferior by progeny tests. A clonal orchard bulk lot collected before roguing and a commercial lot were included in the study, both collected in 1965 by the Georgia Crop Improvement Association (Table 1).

These 36 seed lots were sown in the nursery in 1978 and 1-0 seedlings from them were planted in 1979 on 2 test sites. One was in the Flatwoods in Ware County and one was in the Upper Coastal Plain (UCP) in Houston County, Georgia. At each location, a 16-tree square plot of each seed lot was planted in each of 5 randomized complete blocks, except that lot 3458 (an individual-tree lot) was not planted in Houston County.

Survival, tree height, and presence of rust infection were observed at plantation ages 2, 3, 5, and 10 years. D.b.h. was also measured at age 10. Results for the tenth year are reported here, except that fusiform-rust data reflect the cumulative record. Percentages were transformed to the arcsines of square roots prior to analyses of variance. Analyses were performed on data combined from all seed lots and from lots grouped in the three main categories in table 1 (first-generation clones, second-generation family bulks, and second-generation individual trees). Six contrasts among different kinds of seed lots in the study were constructed and tested for significance. In all analyses, seed lot and planting site were assumed to be random factors.

## Results

Trees planted on the UCP site survived and grew better but became more heavily infected by fusiform rust than did those planted on the Flatwoods site. Other research also has shown the UCP site to be under high hazard to fusiform rust and the Flatwoods area to be low hazard (POWERS et al., 1975).

Table 3. — Analyses of variance of tenth-year data from 3 family or progeny groups, showing mean squares and significance tests, Upper Coastal Plain site.

Source of variation	Degrees of freedom <sup>1</sup>	Trait			
		Survival	Rust-free	Height	D.b.h.
<u>Lots from first-generation clones</u>					
Seed lot	7	703.8959**	807.2779**	0.8374**	1.1083
Error	27	86.3798	94.1004	0.1771	1.0456
<u>Lots from second-generation families</u>					
Seed lot	7	108.7697	329.2475**	0.4226	1.2925**
Error	27	108.5657	62.7445	0.1409	0.2050
<u>Lots from second-generation trees</u>					
Seed lot	14	246.7907*	937.8600**	0.7372**	1.5287**
Error	55	121.6226	106.1370	0.2231	0.5001

\*) Significant at the 0.05 level.

\*\*) Significant at the 0.01 level.

<sup>1</sup>) Error degrees of freedom reflect one missing plot.

Table 4. — Analyses of variance of tenth-year data from 3 family or progeny groups, showing mean squares and significance tests, Flatwoods site.

Source of variation	Degrees of freedom	Trait			
		Survival	Rust-free	Height	D.b.h.
<u>Lots from first-generation clones</u>					
Seed lot	7 <sup>1</sup>	204.8037	305.0436	0.6155	1.1159
Error	27 <sup>1</sup>	133.9478	202.4876	0.8472	1.6028
<u>Lots from second-generation families</u>					
Seed lot	7	290.5164	353.6562	1.3274*	2.2451
Error	28	138.9829	284.3797	0.4336	1.0155
<u>Lots from second-generation trees</u>					
Seed lot	14 <sup>1</sup>	342.2203 <sup>2</sup>	150.8275	1.3066**	1.8865
Error	53 <sup>1</sup>	186.3652 <sup>2</sup>	193.9809	0.5288	1.0880

\*) Significant at the 0.05 level.

\*\*) Significant at the 0.01 level.

<sup>1</sup>) Error degrees of freedom reflect missing plots.

<sup>2</sup>) Error degrees of freedom for survival is 55.

On the UCP site, variation among all seed lots was significant ( $P < 0.01$ ) for all 4 traits (Table 2). On the Flatwoods site, variation among all seed lots was significant ( $P < 0.5$  or 0.01) for 3 traits but not for percentage rust-free. In analyses combining data from both sites, rust-free percentage was the only trait that varied significantly ( $P < 0.01$ ) among seed lots averaged over site. The site x seed lot interaction had significances of  $P < 0.05$  for survival and height and  $P < 0.01$  for the other 2 traits. The correlation of seed-lot means from the 2 sites was statistically significant ( $P < 0.01$ ) only for rust ( $r = 0.51$ ).

In analyses for the 3 progeny groups, lots within group varied significantly for most traits in most groups on the UCP site (Table 3), but only for height in 2 groups on the Flatwoods site (Table 4). Multiple comparison tests among lots within groups are shown in tables 5, 6, and 7 for progenies from first-generation clones, bulked second-

generation families, and second-generation individual trees, respectively.

The coefficient of variation among bulk lots from second-generation families and among progenies from second-generation individual trees was about the same as that among lots from first-generation clones except for the survival and rust-free traits on the UCP site (Table 8). For those 2 traits on that site, second-generation was less than first-generation variation among the clones.

Trait means for the check and bulk seed orchard lots and the groups representing the different stages of selection, along with 6 contrasts among them, are shown in table 9. No contrasts were significant for the Flatwoods site, but 8 were for the UCP site. Of the significant contrasts, 3 showed gains from selection in the rust-free trait and 3 showed gains in height. The original selection involved in establishing the clonal orchard was ineffective in improving resistance to fusiform rust. In fact, there was

Table 5. — Trait means at age 10 years for progenies from first-generation clones of slash pine planted on 2 sites<sup>1)</sup>.

Seed lot	Trait			
	Survival	Rust-free	Height	D.b.h.
	-----Percent-----		m	cm
<u>Upper Coastal Plain</u>				
3439	97.72 a	48.24 a	10.04 a	13.93 a
3445	68.31 b	6.97 b	8.71 b	13.34 a
3450	67.95 b	1.50 b	8.89 b	12.54 a
3455	73.63 b	8.89 b	8.84 b	12.88 a
3460	52.74 b	0.29 b	9.02 b	12.93 a
3464	60.31 b	3.57 b	9.26 ab	13.60 a
3467	61.50 b	15.62 ab	9.09 b	13.36 a
3469	<u>44.22</u> b	<u>3.91</u> b	<u>9.17</u> ab	<u>13.71</u> a
Mean	65.80	11.12	9.13	13.29
<u>Flatwoods</u>				
3439	58.44 a	89.93 a	7.53 a	10.95 a
3445	57.79 a	61.48 a	7.28 a	11.02 a
3450	67.12 a	85.99 a	6.94 a	9.88 a
3455	32.34 a	95.77 a	6.56 a	10.36 a
3460	40.03 a	77.76 a	7.19 a	11.10 a
3464	52.44 a	85.63 a	7.24 a	10.45 a
3467	48.43 a	82.92 a	7.10 a	10.06 a
3469	<u>53.54</u> a	<u>89.52</u> a	<u>6.53</u> a	<u>9.50</u> a
Mean	51.27	83.62	7.05	10.50

<sup>1)</sup> Within a site, means followed by a common letter do not differ at the 0.05 experimentwise significance level, BONFERRONI'S Method.

Table 6. — Trait means at age 10 years for bulked progenies from second-generation families of slash pine planted on 2 sites<sup>1)</sup>.

Seed lot	Trait			
	Survival	Rust-free	Height	D.b.h.
	-----Percent-----		m	cm
<u>Upper Coastal Plain</u>				
3440	76.26 a	39.88 a	9.48 a	14.29 a
3446	79.43 a	14.51 ab	8.94 a	13.23 bc
3451	60.62 a	11.67 b	8.88 a	13.39 abc
3456	70.65 a	22.03 ab	9.58 a	13.45 abc
3461	72.50 a	29.82 ab	9.35 a	14.01 ab
3465	73.95 a	39.04 a	9.50 a	13.84 ab
3468	83.66 a	38.51 a	9.19 a	13.48 abc
3470	<u>67.13</u> a	<u>14.31</u> ab	<u>8.89</u> a	<u>12.65</u> c
Mean	73.02	26.22	9.23	13.54
<u>Flatwoods</u>				
3440	37.75 a	91.15 a	7.18 ab	11.19 a
3446	39.42 a	77.38 a	6.45 b	10.09 a
3451	65.57 a	79.88 a	7.63 ab	10.88 a
3456	38.50 a	91.26 a	6.94 ab	10.41 a
3461	44.53 a	81.86 a	7.08 ab	10.94 a
3465	57.11 a	87.21 a	6.84 ab	10.23 a
3468	70.37 a	97.91 a	8.00 a	11.91 a
3470	<u>59.32</u> a	<u>65.80</u> a	<u>6.60</u> ab	<u>9.88</u> a
Mean	51.57	84.06	7.09	10.69

<sup>1)</sup> Within a site, means followed by a common letter do not differ at the 0.05 experimentwise significance level, BONFERRONI'S Method.

Table 7. -- Trait means at age 10 years for progenies from second-generation individual trees of slash pine planted on 2 sites<sup>1)</sup>.

Seed lot	Trait			
	Survival	Rust-free	Height	D.b.h.
	-----Percent-----		m	cm
<u>Upper Coastal Plain</u>				
3441	94.60 a	47.31 ab	9.44 abc	13.63 ab
3442	86.16 a	60.57 a	9.99 a	14.09 ab
3443	76.58 a	5.95 cd	8.81 bc	12.73 b
3444	87.94 a	42.64 ab	9.46 bc	13.64 ab
3447	62.13 a	7.37 cd	9.59 abc	13.49 ab
3448	80.28 a	11.63 bcd	8.97 abc	13.35 ab
3449	72.73 a	35.56 bc	9.23 abc	14.41 a
3452	61.42 a	17.25 bcd	9.71 abc	14.10 ab
3453	66.69 a	11.87 bcd	8.93 abc	12.70 b
3454	69.07 a	3.31 d	9.09 abc	13.57 ab
3457	84.81 a	42.23 ab	9.31 abc	13.00 ab
3459	71.26 a	5.72 cd	8.72 c	12.85 ab
3462	73.30 a	33.36 abc	9.53 abc	13.95 ab
3463	81.10 a	26.36 a-d	9.91 ab	14.23 ab
3466	<u>83.09</u> a	<u>57.61</u> a	<u>9.24</u> abc	<u>13.27</u> ab
Mean	76.74	27.25	9.33	13.53
<u>Flatwoods</u>				
3441	73.29 a	94.68 a	8.12 a	11.45 a
3442	21.45 a	94.72 a	7.48 ab	10.84 a
3443	59.21 a	83.08 a	7.84 ab	11.19 a
3444	72.57 a	90.29 a	7.84 ab	11.52 a
3447	54.69 a	91.75 a	7.18 ab	10.37 a
3448	50.98 a	91.87 a	7.05 ab	10.19 a
3449	44.46 a	91.29 a	6.53 ab	9.65 a
3452	57.22 a	82.93 a	7.04 ab	10.35 a
3453	32.98 a	75.12 a	6.67 ab	10.28 a
3454	58.66 a	85.71 a	6.96 ab	10.26 a
3457	41.43 a	96.73 a	6.97 ab	10.11 a
3459	28.16 a	93.39 a	6.67 ab	10.11 a
3462	44.49 a	90.77 a	6.96 ab	9.93 a
3463	37.02 a	91.05 a	6.95 ab	9.88 a
3466	<u>54.69</u> a	<u>97.08</u> a	<u>6.32</u> b	<u>9.50</u> a
Mean	48.76	90.03	7.10	10.37

<sup>1)</sup> Within a site, means followed by a common letter do not differ at the 0.05 experimentwise significance level, BONFERRONI'S Method.

Table 8. -- Coefficient of variation among lots within group for 4 traits at age 10 years, slash pine planted on 2 sites.

Group	Trait	Site	
		Upper Coastal Plain	Flatwoods
-----Percent-----			
Progenies from:			
First-generation clones	Survival	47.97	31.30
	Rust-free	171.68	26.09
	Height	10.02	11.13
	D.b.h.	7.92	10.06
Second-generation bulk families	Survival	17.71	37.09
	Rust-free	60.02	27.85
	Height	7.04	16.25
	D.b.h.	8.40	14.02
Second-generation trees	Survival	25.46	40.00
	Rust-free	102.80	17.00
	Height	9.20	16.10
	D.b.h.	9.14	13.24

Table 9. — Means for and contrasts among check and bulk lots and groups for 4 traits at age 10 years of slash pine planted on 2 sites.

Lot, group and contrast	Trait			
	Survival	Rust-free	Height	D.b.h.
	-----Percent-----		m	cm
<u>Upper Coastal Plain</u>				
1. Commercial check	72.65	18.30	8.30	12.09
2. Clonal orchard bulk	56.73	3.28	8.63	13.71
3. First-generation clones	65.80	11.12	9.13	13.29
4. Seedling S.O. bulk (1976)	73.60	31.22	9.82	13.90
5. Second-generation bulk families	73.02	26.22	9.23	13.54
6. Second-generation trees	76.74	27.25	9.33	13.53
2 vs 1	-15.92*	-15.02	0.33	1.62
3 vs 2	9.07	7.84	0.50*	-0.42
4 vs 3	7.80	20.10**	0.69**	0.61
5 vs 3	7.22	15.10**	0.10	0.25
(5 + 6) vs 3	9.08**	15.61**	0.15*	0.25
6 vs 5	3.72	1.03	0.10	-0.01
<u>Flatwoods</u>				
1. Commercial check	58.85	70.19	6.70	10.08
2. Clonal orchard bulk	43.52	69.00	6.47	9.62
3. First-generation clones	51.27	83.62	7.05	10.50
4. Seedling S.O. bulk (1976)	39.72	95.70	6.79	9.96
5. Second-generation bulk families	51.57	84.06	7.09	10.69
6. Second-generation trees	48.75	90.03	7.10	10.37
2 vs 1	-15.33	-1.19	-0.23	-0.46
3 vs 2	7.75	14.62	0.58	0.88
4 vs 3	-11.55	12.08	-0.26	-0.54
5 vs 3	0.30	0.44	0.04	0.19
(5 + 6) vs 3	-1.11	3.42	0.05	-0.03
6 vs 5	-2.82	5.97	0.01	-0.32

\*) Significant at the 0.05 level.  
 \*\*) Significant at the 0.01 level.

a 15% loss compared with the commercial check (2 vs. 1, Table 9, UCP). About half of this loss was regained by roguing the clonal orchard (3 vs. 2). The rogued families in the seedling seed orchard showed gains of 15% to 20% in the rust-free trait compared with the mean for the first-generation parent clones (groups 4-6 vs. group 3, Table 9). Response of the survival trait to selection closely paralleled the response of the rust resistance trait. Selection at all stages was effective in producing gains in height on the UCP site (Table 9).

### Discussion

On the Flatwoods site, fusiform-rust infection pressure was too low to afford a meaningful test for the rust-free trait (GODDARD et al., 1975). Also, site quality variation among and within blocks was noticeably greater there than on the UCP site. For all four traits, error variances were considerably greater for the Flatwoods than for the UCP site (Table 2). This difference in site variation may account for some of the lack of correlation of results between the 2 test sites. Since the UCP proved to be a much better test site than the Flatwoods, especially for rust resistance, results from the UCP should be given more weight than results from the Flatwoods.

Variation in selected traits is expected to decrease with increasing numbers of generations. A decrease in variation in fusiform rust resistance was evident among these slash pines after only 2 generations of selection (Table 8). In this study only the second generation of selection for rust resistance was effective, so the amounts of increase in resistance and decrease in variation are rather remarkable. Only a few generations of selection and breeding may be required to produce a population of slash pine with uniformly high resistance to fusiform rust. Variation in height and d.b.h., however, did not noticeably decrease over 2 generations of selection. Gains over several generations may be possible in these 2 traits. The more genes controlling a trait, the more generations variation persists and are gains possible.

Large gains in both rust resistance and height growth appear to be possible in slash pine. Improvement in the rust-resistance trait, however, requires either that selection be done in stands which have been heavily exposed to the fungus or that progeny tests of selected trees be conducted in areas where the fungus is prevalent. A combination of the two probably would produce the greatest gains.

These 2 test sites probably are near the 2 extremes of fusiform rust hazard level for slash pine in Georgia. One

or more other test sites along the hazard level continuum probably would have given a more clear definition of the progeny x site interaction for rust infection rate. Progeny testing procedures should include extreme and intermediate sites over the area in which seed orchard stock is to be used, so important interactions can be measured. Accurate quantification of interaction effects is essential for the precise genotype/site matching expected in future forestry practices.

The seedling seed orchard approach was effective in improving fusiform-rust resistance and height growth in these slash pine selections. Effectiveness and ease of establishment favor the inclusions of seedling seed orchards in tree improvement programs.

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## Mating System and Effective Pollen Immigration in a Norway Spruce (*Picea abies* (L.) Karst) Plantation

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#### Summary

Mating system and effective pollen immigration in a Norway spruce (*Picea abies* (L.) KARST) plantation were studied using multilocus allozyme markers. The estimated proportions of ovules fertilized by pollen from maternal trees themselves (selfing), from other trees within the plantation (local outcrossing), and from trees outside the plantation (immigration) were 0.09, 0.75, and 0.16, respectively. These estimates varied significantly among trees within the plantation. The majority of selfs (85%) and pollen immigrants (84%) could be attributed to a small proportion of trees (25%). Fifty percent of pollen haplotypes observed in the plantation were due to immigration and most of them likely were contributed by an extraneous population located about 4 km away. These results advance our knowledge about gene flow in conifers and have implications for seed orchard management.

**Key words:** Allozymes mating system, gene flow, Norway spruce, EM algorithm.

#### Introduction

Mating system and gene flow are critical components to theoretical population genetics. They are crucial in determining the spatial genetic structure and evolutionary

potential of natural populations (LOVELESS and HAMRICK, 1984). Information on mating system and gene flow is also of great value in forest tree improvement programs. Inbreeding, particularly selfing, and pollen contamination are the most important factors reducing genetic efficiency of wind-pollinated seed orchards. Therefore, minimizing the degree of inbreeding and pollen contamination is paramount for developing orchard designs and management regimes (ADAMS, 1983; FRIEDMAN and ADAMS, 1982, 1985; SHEN et al., 1981). While substantial effort has been expended in examining mating systems during the past 2 decades (BROWN, 1990; BROWN et al., 1984), there are only a few studies that quantify the level of realized gene flow in forest tree populations (ADAMS and BIRKES, 1990; FAST et al., 1985). Recently, an EM-algorithm procedure has been proposed for joint estimation of mating system and effective pollen immigration parameters in gymnosperm populations (XIE et al., 1991a), enabling the simultaneous investigation of mating system and gene flow.

Norway spruce (*Picea abies* (L.) KARST) is a prominent canopy tree of both boreal and montane conifer-dominated forests in Europe and Asia, and it is one of the most valuable timber tree species in central Europe (SCHMIDT-VOGT, 1977). Despite its commercial importance, information on the level of realized gene flow in Norway spruce populations is not available and knowledge of the mating

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